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Retrieval of the genus *Capitellus* Siddiqi, 1983, with description of *C. caramborum* sp. nov. (Dorylaimida, Belondiridae) associated with Andalusian (Spain) olive groves

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Abstract

A new species of belondirid nematode, collected in olive groves of the southern Iberian Peninsula, is described, including SEM observations and molecular (LSU, SSU) study. *Capitellus caramborum* **sp. nov.** is characterized by its 0.82–1.09 mm long body, lip region offset by constriction and 6.0–6.5 µm wide with a distinct perioral refractive disc 4.0–4.5 µm wide, odontostyle 6.0–6.5 µm long, odontophore bearing basal flanges and 1.8–2.0 times the odontostyle long, neck 223–296 µm long, pharyngeal expansion occupying 53–59% of the total neck length, female genital system diovarian, uterus simple and 27–38 µm or 1.4–1.9 body diameters long, vulva (V = 53–56) longitudinal, tail convex conoid to subcylindrical (24–34 µm, c = 31–38, c' = 1.8–2.1), spicules strongly curved ventrad and 23–25 µm long, and four ventromedian supplements. Morphological and molecular data support the retrieval of *Capitellus* as a valid genus, its taxonomy being updated, including the transference of *Dorylaimellus neocapitatus* to it.

Key Words

Description, dorylaims, LSU, morphology, nematodes, new combination, phylogeny, SSU, taxonomy

Introduction

In his revision of the subfamily Dorylaimellinae Jairajpuri, 1964, Siddiqi (1983) proposed the new genus *Capitellus* to transfer *Dorylaimellus capitatus* Siddiqi, 1964, as its only and type species. Siddiqi (*op. cit.*) also stated that *Capitellus* was (p. 4) unique among the Dorylaimellinae in having a continuous lip region and an angular, "refractive perioral disc," thus putting especial emphasis on the relevance of this peculiar feature as its most recognizable diagnostic trait. Besides, *Capitellus* was characterized by its indistinct perioral sclerotized pieces, diovarian female genital system, and subcylindrical tail. Jairajpuri and Ahmad (1992) admitted *Capitellus* as a valid taxon but lowered its category to a subgeneric level under the genus *Dorylaimellus* Cobb, 1913; meanwhile, Andrássy (2009) considered both taxa to be identical.

Available information about the type and only species, *C. capitatus* (Siddiqi, 1964) Siddiqi 1983, is limited to a rather simple original description and illustrations based on eleven females collected from soil around roots of mango at Kareli, Madhya Pradesh, India. Moreover, Siddiqi (1983) reported its presence in other territories and habitats: Pakistan, lucerne soil in Tanzania, and banana soil in Trinidad; nevertheless, the author did not provide further data about these populations.

Peralta and Peña-Santiago 2000 (see also Jiménez-Guirado et al. 2007) described *Dorylaimellus neocapitatus* from several locations of the southern Iberian Peninsula, Spain, associated with Mediterranean brushwood (*Ulex parviflorus* Pourr., *Echinospartum boissieri* (Sapch) Rothm., *Retama* sp., *Chamaerops humilis* L., *Pistacia lentiscus* L., *Foeniculum vulgare* Mill., and *Lavandula stoechas* Lam.), but also with almond groves

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and a wheat field. This species shared with *C. capitatus* the presence of a refractive perioral disc and other features of their general morphology, but it was easily separable from this in several relevant morphometrics.

Two populations of a Dorylaimellinae taxon were collected in the course of a nematological survey conducted to study the free-living fauna inhabiting olive soils in the framework of the project *Soil O-Live* (EU Horizon Program grant No 101091255). Its morphological and molecular study revealed that it belonged to an unknown form very similar to *C. capitatus* and *D. neocapitatus*. Thus, this contribution aims to describe it, to obtain its molecular characterization, and to discuss its evolutionary relationships. The results are presented in the following.

Materials and methods

Nematodes and their morphological and morphometrical study

A total of 20 specimens found in soils of olive groves were available to study. Nematodes were extracted by centrifugation (CDFA 2015, based on Jenkins 1964) and/or with Baermann's funnels following the protocol by Flegg (1967); somewhat modified, killed by heat, fixed in 4% formaldehyde, preserved in anhydrous glycerin according to Siddiqi's (1964b) method, mounted on permanent glass slides that were sealed with paraffin, and measured and photographed using an Eclipse 80i microscope (Nikon) equipped with differential interference contrast optics, a drawing tube (*camera lucida*), and a DS digital camera. Morphometrics include Demanian indices (de Man, 1880) and other measurements and ratios, some of them presented in a separate table, while others form part of the literal description of species. Two specimens preserved in glycerin were selected for observation with a SEM according to Abolafia (2015). The nematodes were hydrated in distilled water, dehydrated in a graded ethanol–acetone series, critical point dried, coated with gold, and observed with a Zeiss Merlin microscope (5 kV).

Molecular study

For molecular analyses, single specimens were temporarily mounted in a drop of 1 M sodium chloride containing glass beads. This was followed by DNA extraction from single individuals as described by Archidona-Yuste et al. (2016). The D2–D3 domains were amplified using the D2A (5′−ACAAGTACCGTGAGGGAAAGTTG−3′) and D3B (5′−TCGGAAGGAACCAGCTACTA−3′) primers (Nunn, 1992; De Ley et al., 1999). The portion of 18S rRNA was amplified using primers 988F (5′−CTCAAAGATTAAGCCATGC−3′), 1912R (5′−TTTACGGTCAGAACTAGGG−3′), 1813F (5′−CTGCGTGAGAGGTGAAAT−3′), and 2646R (5′−GCTACCTTGTTACGACTTTT−3′) (Holterman et al. 2006). All polymerase chain reaction (PCR) assays were done according to the conditions described by Archidona-Yuste et al. (op. cit.). The amplified PCR products were purified using ExoSAP-IT (Affimetrix, USB products) and used for direct sequencing on a DNA multicapillary sequencer (Model 3130XL genetic analyzer; Applied Biosystems, Foster City, CA, USA), using the BigDye Terminator Sequencing Kit V.3.1 (Applied Biosystems, Foster City, CA, USA), at the StabVida sequencing facilities (Caparica, Portugal) according to the Sanger et al. (1977) method. The newly obtained sequences were submitted to the GenBank database under the accession numbers indicated on the phylogenetic trees.

Phylogenetic analyses

For phylogenetic relationships, analysis was based on 18S and 28S rDNA fragments. The obtained sequences were manually edited using Chromas 2.6.6 (Technelysium) and aligned with other rDNA sequences available in GenBank using the ClustalW alignment tool implemented in MEGA7 (Kumar et al. 2016). Poorly aligned regions at extremes were removed from the alignments using MEGA7. The best-fit model of nucleotide substitution used for the phylogenetic analysis was statistically selected using jModelTest 2.1.10 (Darriba et al. 2012). The phylogenetic tree was generated with the Bayesian inference method using MrBayes 3.2.6 (Ronquist et al. 2012). *Romanomermis culicivorax* Ross & Smith, 1976 (DQ418791 and EF417153, for the 18S and 28S rDNA trees, respectively) was chosen as an outgroup. The analysis under the General Time Reversible plus Invariant sites plus Gamma distribution (GTR + I + G) model was initiated with a random starting tree and run with the Markov chain Monte Carlo (MCMC) (Larget and Simon 1999) for 1×10^6 generations. A total of 25% of samples was discarded as burn-in. The tree was visualized and saved with FigTree 1.4.4 (Rambaut 2018).

Results

Capitellus caramborum sp. nov.

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Figs 1–4

Material examined. Fourteen females and six males from two locations, in variable states of preservation.

Morphometrics. See Table 1.

Description. Baena (type) population:

Adult. Slender (*a* = 40–49) nematodes of small to medium size, 0.82–1.04 mm long. Body cylindrical, tapering towards both extremities. Upon fixation, habitus regularly curved ventrad, often adopting an open C shape. Cuticle dorylaimid, two-layered, thin, *ca* 1 µm thick throughout the entire body, outer layer bearing very fine transverse striation, better observable with SEM.

Table 1. Main morphometrics of *Capitellus* species. Measurements in µm except L in mm, and in the form: average ± sd (range).

Species	***C. caramborum* sp. nov.**				***C. capitatus***	***C. neocapitatus***
Population	**Baena**			**Antequera**	**Type**	**Several**
Country	**Spain**			**Spain**	**India**	**Spain**
	Holotype	**Paratypes**				
n	♀	7♀♀	6♂♂	6♀♀	11♀♀	23♀♀
Character						
L	0.98	0.94 ± 0.05 (0.88–1.04)	0.88 ± 0.05 (0.82–0.94)	1.04 ± 0.50 (0.97–1.09)	0.58–0.65	0.75–0.99
a	47	45.3 ± 3.1 (40–49)	45.3 ± 3.1 (40–49)	48.7 ± 2.3 (44–51)	30–37	35–42
b	3.6	3.7 ± 0.2 (3.5–4.1)	3.7 ± 0.2 (3.5–4.1)	3.7 ± 0.1 (3.6–3.9)	2.7–3.3	2.7–3.7
c	34	35.0 ± 2.3 (31–38)	35.0 ± 2.3 (31–38)	34.0 ± 2.0 (32–36)	21–25	28–39
V	54	54 ± 1.0 (53–56)	–	54.0 ± 1.0 (53–56)	54–56	52–59
c'	2.0	1.9 ± 0.1 (1.8–2.0)	2.1 ± 0.1 (2.0–2.1)	2.1 ± 0.1 (1.9–2.1)	2.2[1]	1.3–1.7
Lip region diameter	6.5	6.3 ± 0.2 (6.0–6.5)	6.3 ± 0.3 (6.0–6.5)	6.3 ± 0.3 (6.0–6.5)	?	6.5–7.5
Odontostyle length	6.0	6.1 ± 0.2 (6.0–6.5)	6.1 ± 0.2 (6.0–6.5)	6.3 ± 0.3 (6.0–6.5)	4.5	5.0–5.5
Odontophore length	12	11.9 ± 0.4 (11.5–12.5)	12.1 ± 0.3 (12–12.5)	12.1 ± 0.5 (11.5–12.5)	13–14	10–12
Neck length	268	253 ± 14 (225–268)	248 ± 25 (223–283)	282 ± 17 (252–296)	217[1]	221–278
Pharyngeal expansion length	143	137 ± 14 (106–155)	134 ± 16 (111–158)	153 ± 19 (118–174)	113[1]	131–159
Body diameter at neck base	21	21.0 ± 0.9 (20–23)	20.1 ± 0.8 (19–21)	21.6 ± 1.1 (20–23)	?	20–26
mid-body	21	20.9 ± 1.0 (20–23)	19.9 ± 0.7 (19–21)	21.3 ± 0.8 (20–22)	20[1]	21–28
anus/cloaca	14	14.9 ± 0.7 (14–16)	15.9 ± 0.5 (15–17)	14.9 ± 0.6 (14–16)	12[1]	15–18
Distance vulva – anterior end	529	512 ± 34 (464–574)	–	562 ± 27 (522–595)	354[1]	420–533
Prerectum length	90	94.5 ± 3.0 (90–96)	72.4 ± 9.9 (58–79)	94.6 ± 3.1 (92–98)	?	62–98
Rectum/cloaca length	19	18.7 ± 1.3 (17–20)	?	19.4 ± 0.2 (19–20)	?	12–18
Tail length	29	27.0 ± 1.7 (24–29)	33.0 ± 1.0 (32–34)	30.6 ± 1.0 (29–32)	26	23–28
Spicules length	–	–	24.3 ± 0.8 (23–25)	–	–	–
Ventromedian supplements	–	–	4	–	–	–

Lateral chord 6.0–6.5 µm wide, occupying less than one-third (26–31%) of mid-body diameter, bearing abundant granular gland bodies. Body pores abundant, appearing as (SEM observations, Fig. 4J) short longitudinal slits. Lip region cap-like, offset by constriction, 1.7–2.0 times as wide as high and up to one-third (28–33%) of body diameter at neck base, with a well-differentiated, refractive perioral disc; SEM observations: lips amalgamated, their inner region visibly offset and somewhat expanded, forming a small sucker-like perioral disc 4.0–4.5 µm wide and divided into six triangular sectors by the existence of six radial, interlabial incisures running from the oral aperture to the margin of the disc, labial and cephalic papillae low, but comparatively large and distinct, button-like, with a coarse pore at their center. Amphid fovea cup-like, its opening 6.0–6.5 µm wide, occupying the entire diameter of lip region. Cheilostom 6.0–6.5 µm long, almost cylindrical, thin-walled, with circumoral sclerotized pieces at its anterior end. Odontostyle typical dorylaimid but small, almost equal (0.9–1.0 times) to lip region diameter long, occupying 0.56–0.66% of body length, *ca* 5.0 times as long as wide, with short aperture *ca* one-fifth of its length. Guiding ring simple, often inconspicuous. Odontophore visibly flanged, 1.8–2.0 times the odontostyle. Pharynx consisting of a slender and weakly muscular anterior region suddenly enlarging into the basal expansion 10–16 times as long as wide, 5.3–8.1 times longer than body diameter at neck base, occupying more than half (53–59%) of the total neck length, and surrounded by a distinct spiral muscular sheath, its gland nuclei and outlets obscure in the specimens examined, some specimens bearing a few refractive globules at its anterior end. Cardia small and rounded, 9–11 µm long.

Female. Genital system diovarian, with both branches equally and variably developed, the anterior 74–122 µm or 8–12% of the total body length, the posterior 87–108 µm or 9–11%. Ovaries comparatively small, often not reaching the oviduct-uterus junction, 31–61 µm the anterior and 36–48 µm the posterior, with oocytes first arranged in two or more rows and then in one single one. Oviduct 42–65 µm or 2.1–3.3 body diameters long, consisting of a long and slender distal region made of prismatic cells and a developed proximal *pars dilatata* with visible lumen. A distinct sphincter present between oviduct and uterus. Uterus a simple tube-like structure 27–38 µm or 1.4–1.9 body diameters long. Vagina extending inwards 8.0–9.5 µm, to less than one-half (38–45%) of body diameter: *pars proximalis* 5.0–6.0 × 6.0–6.5, with almost straight to somewhat convergent walls that are encircled by weak musculature, *pars distalis* 3.0 µm long. Vulva a longitudinal slit *ca* 2 µm long. Prerectum 6.2–6.6, rectum 1.2–1.3 anal body diameters long. Tail convex conoid to slightly subcylindrical.

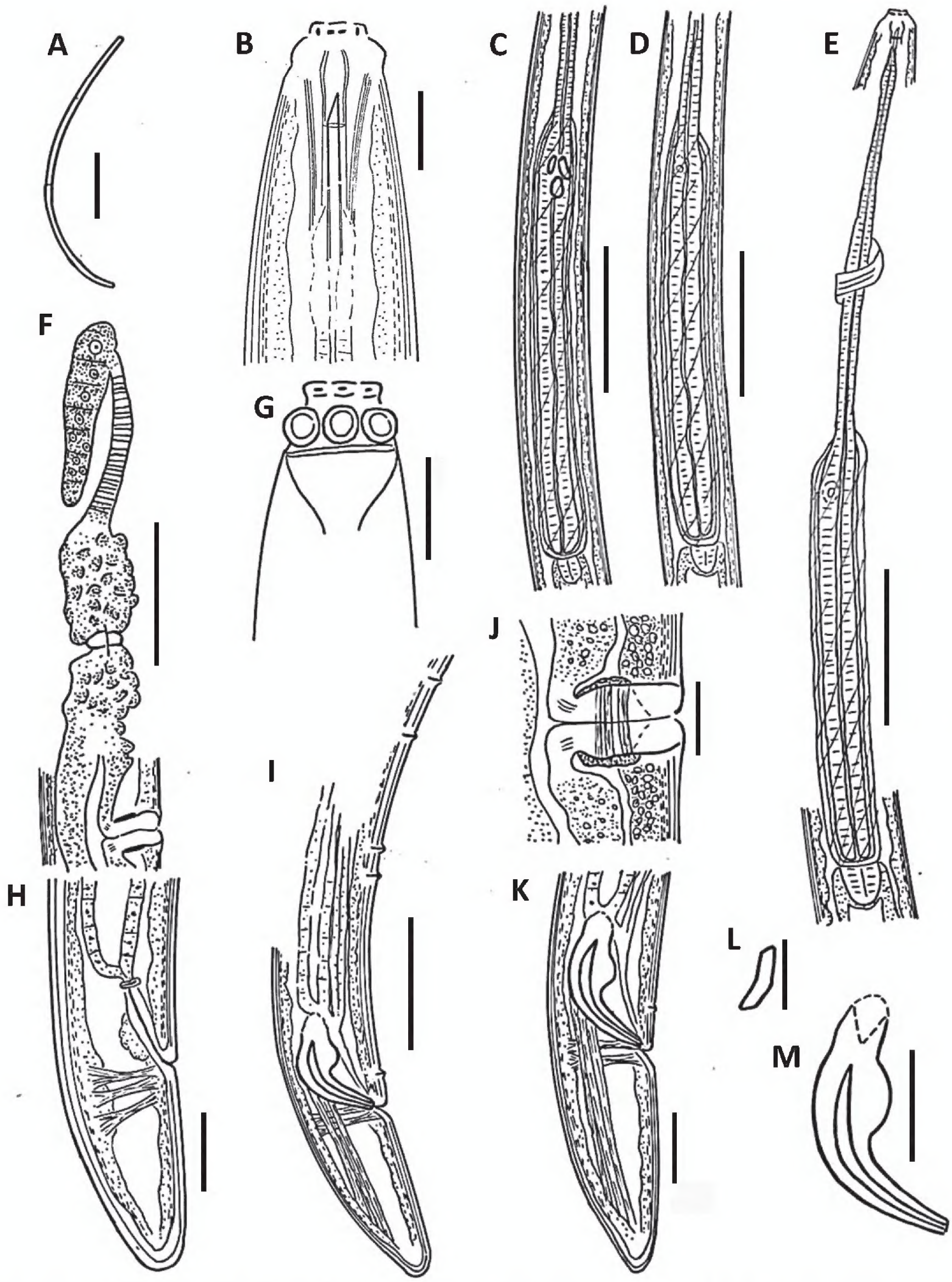

Figure 1. *Capitellus caramborum* sp. nov. **A–H, J.** Female; **I, K–M**. Male; **A.** Entire; **B.** Anterior region, lateral median view; **C.** Pharyngeal expansion with globules; **D.** Pharyngeal expansion without globules; **E.** Neck region; **F.** Anterior genital branch; **G.** Anterior region, lateral surface view; **H, K.** Caudal region; **I.** Posterior body region with ventromedian supplements; **L.** Lateral guiding piece; **M.** Spicule. Scale bars: 200 µm (**A**); 5 µm (**B, G, J, L**); 50 µm (**C–E**); 25 µm (**F, I**); 10 µm (**H, K, M**).

Male. Genital system diorchic, with opposite testes. In addition to the adcloacal pair, situated at 4–5 µm from the cloacal aperture, there invariably are four very simple (non-mammiform but a low pore-like structure, Fig. 4I) ventromedian supplements arranged in a more posterior pair located at 38–41 µm from the ad-cloacal pair and two more anterior and spaced ones at 23–25 µm from the posterior pair. Spicules dorylaimid, strongly curved ventrad,

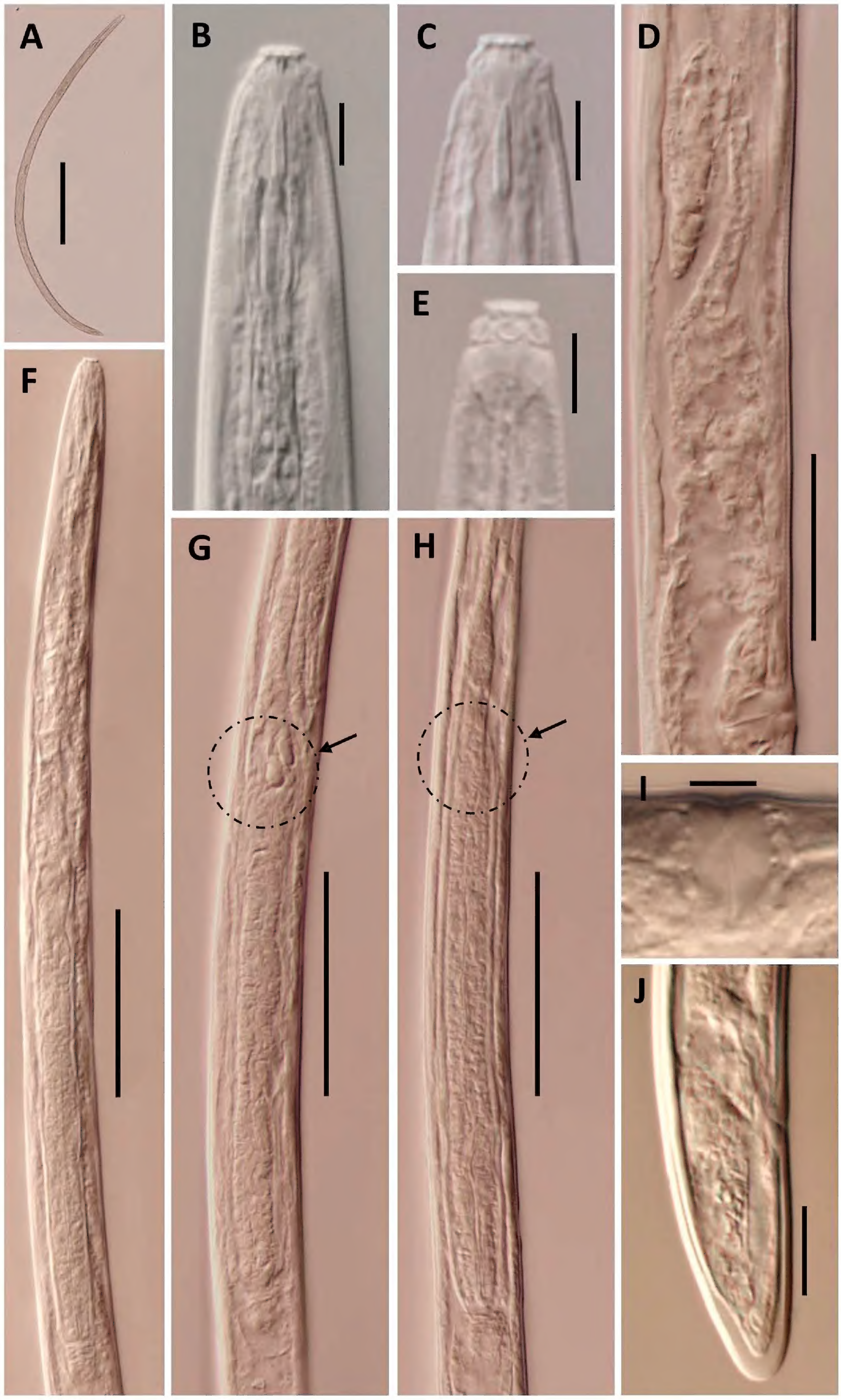

Figure 2. *Capitellus caramborum* sp. nov. (Female, LM). **A.** Entire; **B, C.** Anterior body region, lateral median view; **D.** Anterior genital branch; **E.** Anterior region, lateral surface view; **F.** Neck region; **G.** Pharyngeal expansion with globules; **H.** Pharyngeal expansion without globules; **I.** Vagina region; **J.** Caudal region. Scale bars: 200 µm (**A**); 5 µm (**B, C, E, I**); 25 µm (**D**); 50 µm (**F, G, H**); 10 µm (**J**).

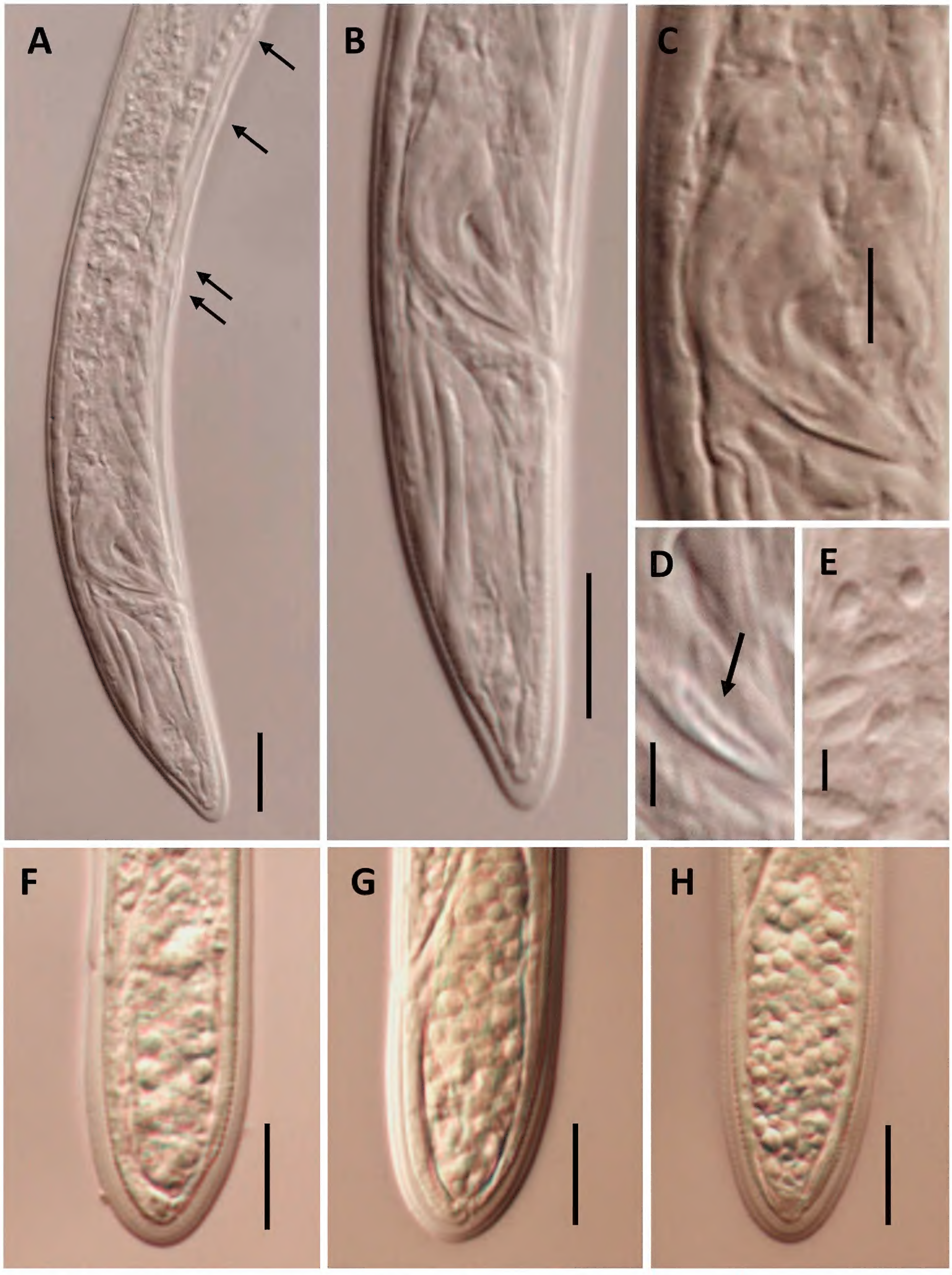

Figure 3. A–E. *Capitellus caramborum* sp. nov. (Male, LM). **A.** Posterior body region, with arrowheads pointing at ventromedian supplements; **B.** Caudal region; **C.** Spicule; **D.** Lateral guiding piece; **E.** Sperm cells; **F–H.** *Capitellus neocapitatus* (Peralta & Peña-Santiago, 2000), comb. nov.; **F–H.** Female tail. Scale bars: 10 µm (**A, B, F–H**); 5 µm (**C**); 2 µm (**D, E**).

Figure 4. *Capitellus caramborum* sp. nov. (SEM). **A.** Lip region, lateral view; **B.** Lip region, in face view; **C.** Vulva, ventral view; **D, E.** Perioral disc, in face view; **F.** Vulva region, lateral view; **G.** Female caudal region, subventral view; **H.** Cloacal aperture and ad-cloacal genital papillae; **I.** Detail of ventromedian supplement; **J.** Caudal pores of female tail. Scale bars: 1 µm (**A, B, D, E, I, J**); 2 µm (**C, F, H**); 5 µm (**G**).

3.7–4.1 times as long as wide and 1.4–1.7 times longer than body diameter: head 3.0–3.5 µm long, up to one-sixth (13–15%) of spicule length, and almost as long as wide; median piece occupying less than one-third (15–31%) of maximum width; ventral hump and hollow very prominent, the former located at 7.5–9.0 µm from the anterior end; curvature 127–128°. Lateral guiding piece simple, 6 µm long. Tail somewhat less convex conoid than that of female.

Antequera population. Females are morphologically identical and morphometrically very similar to those of the type population, as the ranges of their more relevant measurements and ratios are coincident or widely overlap. No male found.

Molecular characterization. After sequencing and editing, four sequences were obtained for phylogenetic analyses. Two 18S rDNA sequences, 1719 bp in length (acc. PQ877190–PQ877191), showed 98.14% identity to a sequence (AY552969) assigned to *Dorylaimellus virginianus* Cobb, 1913 (Jairajpuri & Ahmad, 1980) and 97.85%, 97.62%, and 98.02% identity to sequences assigned to *D.*

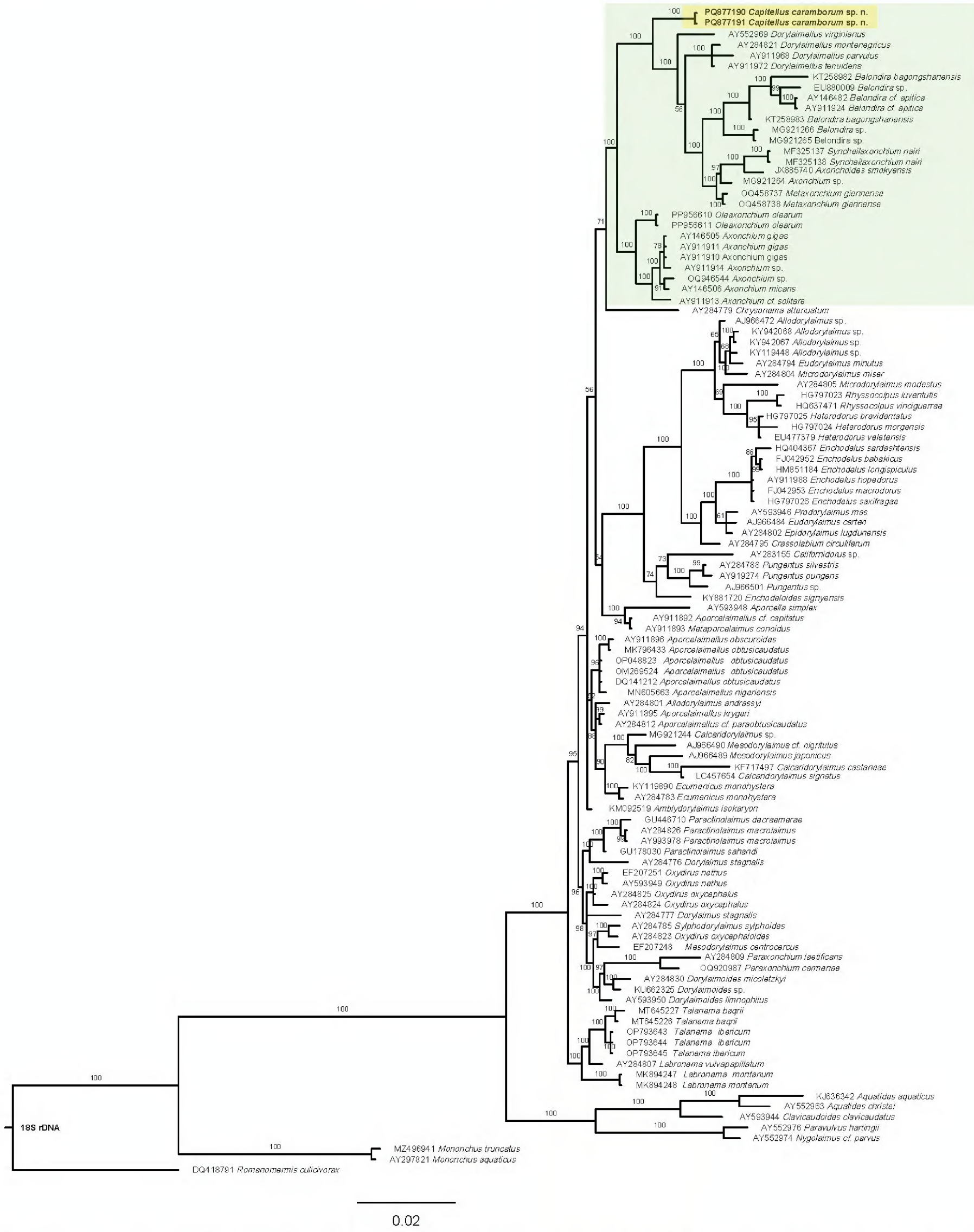

Figure 5. Bayesian inference tree from the newly sequenced *Capitellus caramborum* sp. nov. based on sequences of the 18S rDNA region. Bayesian posterior probabilities (%) are given for each clade. The scale bar shows the number of substitutions per site.

montenegricus Andrássy, 1959 (Jairajpuri & Ahmad, 1980), *D. parvulus* Thorne, 1939 (Jairajpuri & Ahmad, 1980), and *D. tenuidens* Thorne, 1939, respectively (AY284821, AY911968, and AY911972).

Two 28S rDNA sequences, 793 bp in length (acc. PQ877192–PQ877193), showed 83.61% identity to two sequences (KT258984, KT25985) assigned to *Belondira bagongshanensis* Wu, Huang, Xie, Wang & Xu, 2017, 91.14% to those of *Belondira* sp. (MG921267, MG921268), and 80.71% identity to *B. coomansi* Golhasan, Heydari, Miraeiz, Abolafia & Peña-Santiago, 2018 (MF363124).

Diagnosis. The new species is characterized by its 0.82–1.09 mm long body, lip region offset by constric-

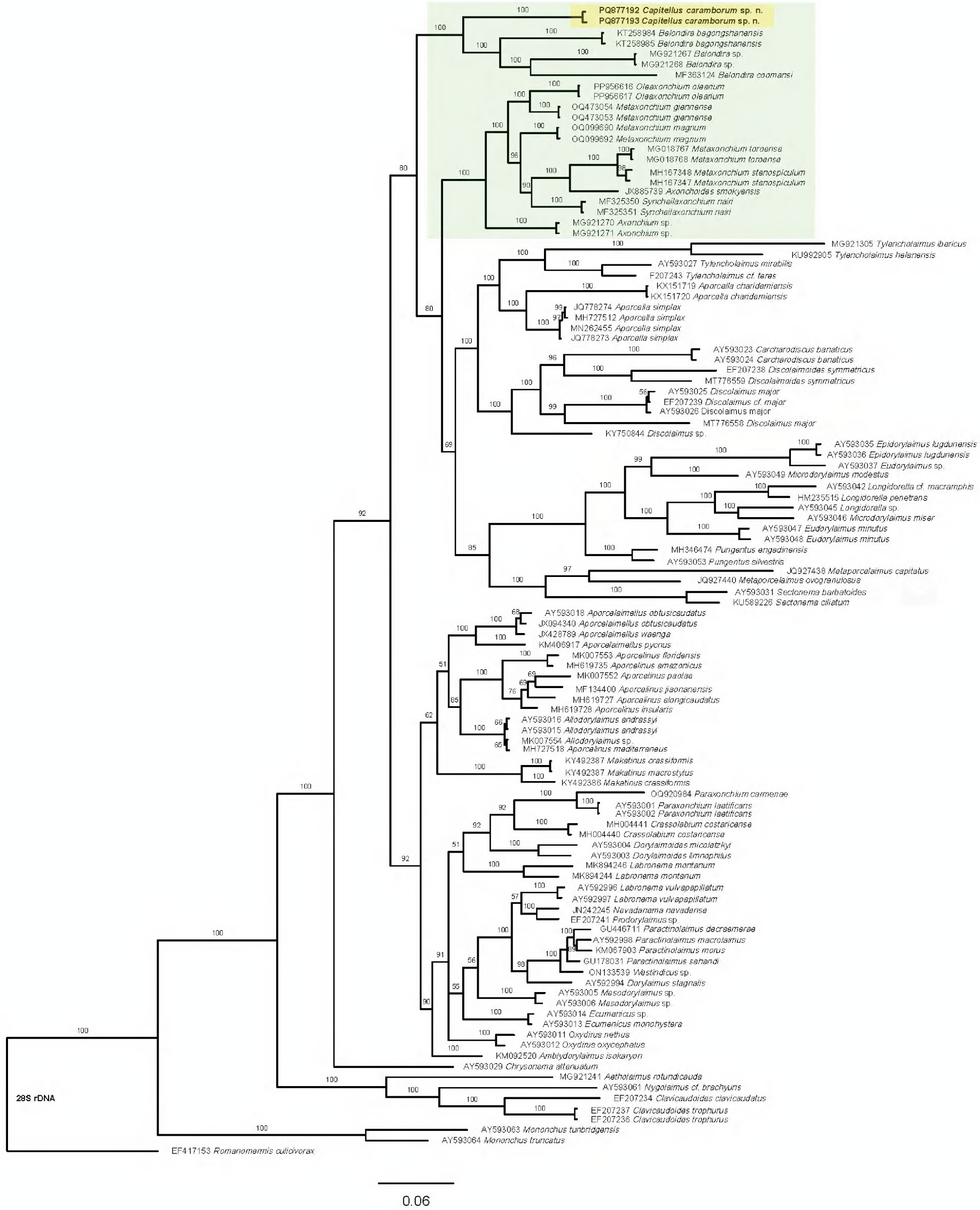

Figure 6. Bayesian inference tree from the newly sequenced *Capitellus caramborum* sp. nov. based on sequences of the 28S rDNA region. Bayesian posterior probabilities (%) are given for each clade. The scale bar shows the number of substitutions per site.

tion, and 6.0–6.5 µm wide with a distinct perioral refractive disc 4.0–4.5 µm wide, odontostyle 6.0–6.5 µm long, odontophore bearing basal flanges and 1.8–2.0 times the odontostyle long, neck 223–296 µm long, pharyngeal expansion occupying 53–59% of the total neck length, female genital system diovarian, uterus simple and 27–38 µm or 1.4–1.9 body diameters long, vulva (V = 53–56) longitudinal, tail convex conoid to subcylindrical (24–34 µm, c = 31–38, c' = 1.8–2.1), spicules strongly curved ventrad and 23–25 µm long, and four ventromedian supplements.

Separation from its relatives. The new species is similar to *C. capitatus* and *D. neocapitatus*. It differs from *C. capitatus*, a mainly pantropical taxon, in its lon-

ger (0.82–1.09 *vs.* 0.58–0.65 mm) and slender (*a* = 44–51 *vs. a* = 30–37 in females) body, lip region offset by constriction (*vs.* almost continuous), larger odontostyle (5.5–6.5 *vs.* 4.5 µm), comparatively shorter tail (*c* = 31–38 *vs. c* = 21–25), and male present (*vs.* absent). From *D. neocapitatus*, a very close taxon, in its narrower lip region (6.0–6.5 *vs.* 6.5–7.5 µm wide, n = 21), longer odontostyle (6.0–6.5 *vs.* 5.0–5.5 µm) – it means that the odontostyle is almost equal *vs.* appreciably shorter than lip region diameter –, relatively shorter pharyngeal expansion (53–59 *vs.* 59–63% of the total neck length), more conoid (*vs.* more subcylindrical, Fig. 3F–H), and comparatively longer female tail (*c'* = 1.8–2.1 *vs. c'* = 1.3–1.7), and male present (*vs.* absent).

Type locality and habitat. Southern peninsular Spain, the Andalusia region, Córdoba province, Baena municipality, "El Valle" farm (37.799704, -4.310439, elevation 351 m), where the new species was found in the rhizosphere of an olive grove.

Other locality and habitat. Southern peninsular Spain, the Andalusia region, Málaga province, Antequera municipality, "La Capilla" farm (37.198283, -4.543868, elevation 491 m), where the new species was found in the rhizosphere of an olive grove.

Etymology. The specific name refers to the "Carambos," the familiar nickname of the first author's mother.

General discussion

Morphologically, *C. caramborum* sp. nov. forms a recognizable group of species together with *C. capitatus* and *D. neocapitatus*, all of them easily distinguishable by having a distinct perioral disc visibly refractive, which should be regarded as a very relevant synapomorphy (if not autapomorphy) in Dorylaimellinae. Besides, the general morphology of the three species is nearly identical, and their morphometrics (Table 1) are rather similar too.

Unfortunately, molecular studies of Dorylaimellinae representatives for comparison are limited to a few 18S-rDNA and no 28S-rDNA sequences. Thus, the evolutionary relationships of the new species as derived from the analyses whose results are presented in trees of Fig. 5 (18S-rDNA) & 6 (28S-rDNA) only confirm its belonging to maximally supported (100%) clades constituted by members of Belondiridae Thorne, 1939 (highlighted in green in both trees), excepting *Oxydirus* Thorne, 1939 sequences. Nevertheless, this clade includes all Belondiridae representatives in the 18S tree, while the 28S tree only contains *Belondira* sequences.

Present findings support the idea that *Capitellus* is a valid taxon. On the one hand, the new species now described is the third one displaying a very unusual (?unique) feature within Dorylaimellinae, and it forms a recognizable group with two previously known forms. On the other hand, the 18S tree shows that the two sequences of the new species form a clade that is separated from that including other *Dorylaimellus* species, which form part of another clade together with several belondiirid taxa. Thus, *Capitellus* is provisionally recovered as a valid genus, and, consequently, *D. neocapitatus* is transferred to it.

Updated taxonomy of *Capitellus*

Diagnosis

Small-sized nematodes, 0.58–1.09 mm long. Cuticle dorylaimid. Lip region continuous with the adjoining body or offset by weak constriction, with fused lips displaying a conspicuous, perioral, refractive disc. Amphid fovea cup-like, with large aperture. Cheilostom with variably perceptible perioral sclerotized pieces. Odontostyle dorylaimid, up to as long as lip region diameter. Guiding ring simple. Odontophore bearing flanged base. Pharyngeal expansion occupying one-half to two-thirds of the total neck length. Female genital system di-ovarian, with longitudinal vulva. Female tail conoid to subcylindrical. Spicules dorylaimid. Four variably spaced ventromedian supplements with hiatus.

Type species:
C. capitatus (Siddiqi, 1964) Siddiqi, 1983
= *Dorylaimellus capitatus* Siddiqi, 1964
= *Dorylaimellus* (*Dorylaimellus*) *capitatus* Siddiqi, 1964 (Jairajpuri & Ahmad, 1980)
= *Dorylaimellus* (*Capitellus*) *capitatus* Siddiqi, 1964 (Jairajpuri & Ahmad, 1992)

Other species:
C. caramborum sp. nov.
C. neocapitatus (Peralta & Peña-Santiago, 2000), comb. nov.
= *Dorylaimellus neocapitatus* Peralta & Peña-Santiago, 2000

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